

Mortality and Survival in the Laysan Albatross, *Diomedea immutabilis*¹

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ABSTRACT: A 13-year study of 27,667 banded Laysan Albatrosses, *Diomedea immutabilis*, on Midway Island, North Pacific Ocean, provided specific mortality rates for each stage of the life cycle.

Egg loss among 6,543 nests averaged 3 to 6 percent in the 1st month of incubation and reached 25 percent during the 2nd month in some seasons. Chick losses ranged from 3 to 17 percent of the eggs laid and occurred more or less evenly from hatching to fledging. Most egg losses were occasioned by desertions by adults, and most deaths of chicks occurred when one or both parents died.

Approximately 3.5 percent of 4,492 banded, departing fledglings died of starvation and exhaustion on the beaches. Losses to sharks in the nearby waters were thought to increase fledgling mortality to perhaps 10 percent before the surviving young birds reached the open sea.

A mean 6.8 percent of 7,000 juveniles were lost in each of the first 4 years at sea, but in each of the next 4 years, when the birds were more experienced and had spent more time in the colonies where there were no natural predators, annual mortality averaged only 1.8 percent.

Young breeders had a mean annual mortality of 3.7 to 4.0 percent in their first nine breeding seasons, whereas a total of 3,305 breeders of all ages had a mean annual mortality of 5.3 to 6.3 percent. There was no consistent sexual variation in mortality of breeding birds, but in 2 years of low breeding populations females experienced greater losses.

Prior to the 14th year of life, the stresses of reproduction were perhaps more significant mortality factors than was age. Age may have been a factor after this, but not until the years after 20 was there any indication of increased mortality.

Approximately 40 percent of the breeding albatrosses lived to a minimum of 12 years, 30 percent to 14 years, 25 percent to 16 years, 20 percent to 18 years, and 13 percent to 20 or more years.

Laysan Albatrosses may have a breeding life expectancy of some 16 to 18 years.

THE PURPOSE of this investigation was to determine specific mortality rates for each stage of the life cycle of the Laysan Albatross, *Diomedea immutabilis*. Underlying this purpose was my desire to present high quality, primary data for comparative use by statistically minded ornithologists and "model-building" ecologists in general. As Hickey (1972: 27) noted, the lack of good, primary information is all too evident in many reports.

No attempt is made here to assess in depth all the factors causing mortality or to theorize about the implications of differential mortality upon the dynamics of the species. Almost nothing is known of the life of the Laysans at sea, where most of their lives are spent, and emphasis must lie on the mortality factors on land.

The Laysan Albatross is an excellent subject for studies of survival. From hatching it is firmly attached to a site within the colony, and it is predictably present there after the age of approximately 4 years. It occurs in large numbers on the breeding grounds, is docile, not

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easily frightened out of the colony, and is simply captured by hand. Pairing is monogamous for the life of the members. All these attributes contribute to the acquisition in successive years of information on large samples from the same cohorts. Data on the same individuals may be obtained for many successive years. For example, 10 to 20 percent of the chicks of 1961–1963, banded for this study, will still be found in their colonies in 1985, as this paper demonstrates.

The investigation, part of a long-term inquiry, was conducted on Midway Atoll, North Pacific Ocean, from June 1961 to January 1973, after a 2-week feasibility study in December 1959. The atoll lies at lat 177° N, long 271° W and consists of two, flat coral islands resting on a reef that surrounds a lagoon some 5 miles in diameter. Sand Island has approximately 1,200 acres and Eastern Island about 400.

In any interpretation of data relating to survival, the immediate past history of the colony and of its site is important. Especially is this true when the area has perhaps one-third of the world's breeding population of the species, when the site has undergone major topographical disruptions, when the species is long-lived (H. I. Fisher 1975a), and when the individuals are so closely and permanently attached behaviorally to their home islands, home colonies, and individual territories (H. I. Fisher and M. L. Fisher 1969, H. I. Fisher 1971a, b).

Laysan Albatrosses bred, relatively undisturbed, on Midway until the late 1930s. At that time, construction of a military base, including airplane runways extending the full length of both islands, the addition of dredged material to the southeast part of Sand Island, and the erection of dozens of buildings, almost completely disrupted the breeding grounds. These activities and those of thousands of military personnel living on the islands, not to mention the bombings and fires of actual warfare, caused the deaths of thousands of albatrosses (Woodbury 1946, H. I. Fisher and Baldwin 1946, H. I. Fisher 1949).

These disastrous conditions continued until the end of World War II in the late summer of 1945. Although the effects of some disturbances

lingered on, the birds were relatively undisturbed for 10 years, until Sand Island became a base for radar planes operating in the Pacific. This new military activity had significant impacts on the colonies on Sand Island (H. I. Fisher 1966a). When the use of the radar base was discontinued in the spring of 1965, major destructions of the albatrosses and their habitat came to an end.

However, it is further necessary to note some specific conditions surrounding the colonies used in this research. The exact locations of the areas and colonies may be found in H. I. Fisher (1971b) and H. I. Fisher and M. L. Fisher (1969). Despite the fact that Sand Island has been the site of the primary human use of Midway's surface since World War II, the colony of albatrosses using the main antenna field (Antenna Field 1 of this study) has suffered few depredations of any kind except the loss of birds as they approached the colony across the runway to the south. The young birds of our investigations were still at sea until after the cessation of the radar flights, and we included no Sand Island adults of this period.

The surface of Eastern Island was completely modified during World War II. Runways, sand and coral bunkers, and buildings and roads then covered most of Eastern Island. Gradually, these modifications were eliminated, except for the concrete runways, and human use decreased until today (1973) only half a dozen navy men work on Eastern. A new mortality factor was introduced in the early 1960s, the high antennas for a system of military communications (H. I. Fisher 1966b, 1970). These destructors, which were only a few hundred yards away, increased the mortality of albatrosses in our study plot.

When I first visited the future site of the plot in May 1945, there were few Laysans present. Only an occasional chick crouched between vehicles or squatted in the sand atop the bunkers in the west edge of the plot. In December 1946 the plot had numerous nesting albatrosses, and it was evident that not all Laysans "belonging" to the plot had fallen victim. We now realize that the adolescent period and breeding life of the Laysan are sufficiently long to span disruptive periods of 8 to 15 years. The breeding birds not actually killed returned to breed in the plot in subsequent years, and the young

that hatched there preceding the disturbances spent most of their growing-up time at sea and returned only to breed.

In the years following my 1946 visit, wind blew sand over the hard-packed area formerly used for parking airplanes. Shrubs, a few casuarina trees, and a tough, introduced weed invaded the plot. In 1959 the site was essentially indistinguishable from those of successful Laysan Albatross colonies on undisturbed islands such as Pearl and Hermes Reef and Lisianski Atoll. The plot has not since been disturbed in any significant way, other than by our yearly studies.

The area we designate "South of Pier" on Eastern Island, and which we also used extensively in these investigations, has a similar history. However, its nearness to the shipping pier, the only entrance to Eastern Island, has resulted in greater, incidental human disturbance of the birds.

This brief chronology of events in the colonies, when combined with the chronology of the Laysan's life, demonstrates, I think, that the colonies and birds currently may be as typical of a "normal" situation as possible. However, the populations of breeding birds have increased in the last dozen years, which must be kept in mind when analyzing the data.

THE LITERATURE

There are only a few reliable studies on the mortality rates and survival of avian species (Hickey 1972), and I make no attempt to review them here. Later reference will be made where pertinent. Most published information, at least that which I have seen, was based upon inadequate samples followed for too few years. In most instances only crude mortality rates were presented, without sufficient attention being paid to the biological stage of the individuals or to possible sexual and annual variations. These critical comments are directed less at the authors than at the problems of time, energy, funds, and the species studied. Not all these problems were overcome in the present study.

Little had been published until recently on mortality, survival, or longevity of the Laysan Albatross (H. I. Fisher, 1975*a, b*). There are, of

course, limited and anecdotal accounts of the ravages of plume hunters and waves, of war-time activities, of antennas, etc. Hadden (1941), Sheehan (1951), Rice (1959), and I (1971*a*: 70–72) have commented upon some aspects of hatching success and nest mortality. Rice and Kenyon (1962: 372) recorded a "nest mortality of 6 per cent per month," and (p. 383) suggested that no more than 8.6 percent of the breeders die annually.

MATERIALS AND METHODS

The details of banding, recapture, sample sizes, and dates are given later, but some general statements are pertinent to all samples.

Definitions

Fledgling: Young within 1 month of departure from the island.

Juvenile: Bird that has gone to sea but has never bred.

Inexperienced breeder: Bird breeding for the first time.

Experienced breeder: Bird known to have nested at least once.

Breeding season: From egg-laying in November of 1 year to departure of fledglings the following summer.

Age: Period between the date the egg was laid and the latest recapture of the bird hatched from that egg. A chick hatched in January 1970 from an egg laid in November 1969 becomes 2 years old in January 1971. All breeders of unknown age were assumed to be a minimum of 8 years old (VanRyzin and H. I. Fisher, unpublished).

Mortality rate: The number dying in a given interval divided by the number in the original sample. The usual method of dividing the number of deaths by the number of survivors at the beginning of any interval of risk emphasizes death rates during the various phases of the life history, which can be quickly determined from my data. My system highlights the successive, percentage loss of life from a constant sample—eggs laid, chicks hatched or fledged, etc.—and is

thus more satisfactory, I think, in considering total survival of populations.

Survival: All periods of survival are minimal since length of life was measured only to the date of last recapture.

The Areas

The survival of known-age birds was studied in Antenna Field 1 and Officers' Country on Sand Island and the Quarters and South of Pier areas on Eastern Island. These areas were used as replicates of each other and provided a better opportunity for a realistic interpretation of certain variables. Antenna Field was flat, mowed several times a year, and lighted in several places on its periphery. Some birds, particularly younger juveniles, flew away from us here, but all birds with bands were easily seen. The Officers' Country site was around the barracks and homes of the officers and had many tall casuarina trees, shrubs, and buildings. The albatrosses were well protected from molestation over the years and were easily recaptured. The Quarters area surrounded the few navy buildings still on Eastern and was flat and rocky. We often had trouble recapturing birds here; even at night the lights of the buildings made it possible for these essentially diurnal birds to fly from us. South of Pier had tall weeds, brush, some trees, and a string of World War II bunkers. Few birds escaped recapture, but we may have overlooked some in any one search.

The plot on Eastern Island, for the most part, was used to study the survival of breeding birds of unknown age, but data on survival of chicks hatched there were included.

Banding

More than 23,000 Laysan Albatrosses had been banded on Midway prior to our study. We banded nearly 50,000 more, and many thousands have been banded by others since 1960, but we could not determine how many. Since it was not feasible to include all the birds we had banded, we concentrated on samples considered adequate in size and in the manner in which they were obtained.

Recapturing

The efficiency and reliability of our recapture data were increased by: (1) the banding of successive year-classes in a few, clearly defined areas; (2) the proclivity of Laysans to return to the same island, colony, and territory each year; (3) the intensity and frequency of our searches in each of 12 years; (4) the fact that we made 99 percent of the recaptures reported and, thus, did not depend upon incidental recaptures by others, as most previous researchers have been forced to do; (5) the ease with which these albatrosses may be caught; (6) the inclusion of the same group of individuals in successive age cohorts (in several samples the same albatrosses were followed from the egg stage through the young breeder's phase); (7) the fact that the 1972-1973 season was by chance an excellent one in which to terminate a study of survival (breeding populations were the largest we have ever recorded, and we could assume, first, that prebreeding season conditions at sea must have been satisfactory, and, second, that maximum numbers of survivors of all ages beyond 6 years had returned); and (8) albatrosses were recaptured during a long span of years, including seasons judged to be "good" as well as "bad" for albatrosses (we observed major annual fluctuations in the breeding populations in two study areas; in 1964 and 1968, for example, they dropped as much as 50 percent, and then rebounded to even greater numbers).

The completeness of our search for nonbreeding birds was indicated by the few additional birds taken near the end of each search period; each recaptured bird received a paint mark on its head to facilitate recognition and to prevent its being disturbed further. We estimated that we missed fewer than 1 percent of the birds 4 or more years of age.

The information on the survival of breeding birds was even more complete. We had the recapture data, gleaned by daily searches of the plot; but also, because we knew the mates of virtually all breeders, because strict monogamous pairing is the rule, and because survivors of broken pairs do not usually breed the first year after the break (H. I. Fisher, unpublished), the presence of one member of

the pair often assured us of the survival of the other member.

In all instances, birds missed in 1 or more years but recaptured later were added to the survivor lists for all previous years. The only significant omissions might represent females that after losing a mate moved to a male outside the searched areas. However, we regularly searched the borders of the areas, and the close similarity in the mortality rates for males and females leads us to believe we did not miss significant numbers of females.

Loss of Bands

We think the loss by albatrosses of properly applied, newer style bands is negligible, at least in the first 10 years. Albatrosses do not appear to be bothered by bands; they do not peck or pull at bands, acts leading Poulding (1954) to suspect that perhaps half of all loss of "butt-end" bands on Herring Gulls, *Larus argentatus*, was due to active removal by the birds. Ludwig (1967) also noted active removal in Ring-billed Gulls, *Larus delawarensis*.

Most of our plot sample of breeding Laysans was rebanded 5 years after the initial banding, and both band numbers were recorded at each subsequent recapture. A random sample of 500 of these, checked at the end of a second 5-year period, revealed that only four of the original and one of the second bands had been lost. There is, of course, the unlikely possibility that both bands may have been lost.

We have no evidence that suggests a sexual difference in loss (Mills 1972), and sexual similarity in behavior on land leads us to discount this possibility.

Our frequent recapture of many of the same birds (oftentimes each year), tightening of loose bands, repair of twisted ones, replacement of those beginning to show wear, and the addition of second bands on most breeders in the plot eliminated any significant bias due to band loss.

Bands on albatrosses often show a great deal of wear in 5 or 10 years, especially if they have been flattened at application and cannot rotate freely on the tarsometatarsus. The same surface is always in contact with the sand and coral when the bird rests or incubates. Fortunately,

many of these worn bands can be deciphered in the laboratory. What is most distressing is to be unable to read bands which, by shape, lock style, or prefix number, can be identified as ones applied many years earlier. Thirty-seven such bands were replaced during this study.

The Samples

Although we made more than 125,000 recaptures of Laysans, we include data on only approximately 62,000 recaptures of 11,548 different individuals in samples totalling 27,667 albatrosses banded and on the fate of 6,543 eggs.

All data have been recorded in the laboratory on individual Key Sort cards maintained for each banded albatross.

MORTALITY OF EGGS AND CHICKS IN NESTS IN THE PLOT: Sample 1 consisted of 2,303 eggs laid from 1961 through 1964 and followed through to chick fledging the next June and July. Sample 2 included 2,787 eggs laid in 1962, 1963, 1964, 1966, and 1968 and checked for hatching success. Sample 3 was of 1,453 eggs laid in 1964, 1966, and 1968 and checked for hatching success and for survival of chicks to the banding age of 6 to 8 weeks.

All nests or chicks were checked (1) daily during the egg-laying period (15 Nov to 15 Dec) in all years; (2) daily during the hatching period in 1962 to 1964, 1966, and 1968 seasons; (3) once a week for banding of chicks in late March and early April of 1964, 1966, and 1968 seasons; and (4) repeatedly from 15 June to 1 August of 1961 through 1964.

MORTALITY OF FLEDGLINGS: The sample consisted of 4,492 fledglings banded in the colonies on Eastern Island in June and July 1963 and recovered on the beaches between 3 and 30 July 1963. The beaches were searched each morning and all living and dead birds were recorded by band number (H. I. Fisher and M. L. Fisher 1969: 186–189). Sex was not recorded because reliable, external determination in other than breeding Laysans is nearly impossible.

MORTALITY OF JUVENILES: Fledglings were banded in marked areas on both islands in 1960

through 1962. These areas were searched at least twice weekly, by day or night or both, and all banded albatrosses were recaptured in the following periods:

1964-1965: 1 Nov 64 to 1 June 65
 1965-1966: 25 Nov to 15 Dec 65
 1966-1967: 25 Nov to 13 Dec 66
 1967-1968: 22 Nov to 15 Dec 67
 1968-1969: 18 Nov 68 to 18 Mar 69
 1969-1970: 17 Nov to 13 Dec 69
 1970-1971: 20 Nov to 15 Dec 70
 1971-1972: 14 Nov to 12 Dec 71
 1972-1973: 19 Nov 72 to 3 Jan 73

The search for returning juveniles was not begun until 1964 because it had been determined earlier that relatively few birds less than 4 years of age do return (Robbins, unpublished; H. I. Fisher and M. L. Fisher 1969: 195-197). Sex was not recorded, for reasons stated above.

Twenty samples from widely dispersed areas were originally included in this portion of the study, but human disturbance over the next dozen years destroyed the usefulness of six areas. The samples from undisturbed areas totalled 7,000 albatrosses and the survivors were recaptured a total of 25,488 times. The samples were combined by year for comparisons of annual variations.

Sample 1 (1960) contained 684 young on Sand Island and 845 on Eastern; sample 2 (1961) was of 1,501 young on Sand and 870 on Eastern; and sample 3 (1962) consisted of 3,100-2,000 from Sand and 1,100 from Eastern.

MORTALITY OF YOUNG BREEDERS: The data are from H. I. Fisher (1975b).

MORTALITY OF EXPERIENCED BREEDERS OF UNKNOWN AGES: Three samples of Laysans banded on Eastern Island included: sample 1 (plot)—917 males and 988 females banded on eggs from 1960 through 1963. Because no selective banding had been done previously in this area, these birds represented a cross-section of all breeding ages. The plot was searched daily during the egg-laying periods of all years of the study, as well as during the searches listed above for juveniles. The annual mortality was calculated for each sex. Sample 2—700

birds banded on eggs in the central part of South of Pier in the 1963-1964 season. Sample 3—700 albatrosses banded on eggs in the west portion of South of Pier in the same season.

Samples 2 and 3 were thus from the same area where the samples of juveniles were located, and the data were gathered in the same way and simultaneously. All breeding ages are believed to have been represented. To make the samples as complete as sample 1, so that valid comparisons with the plot sample might be made, a special effort was made to recapture these breeding birds in the 1968, 1971, and 1972 seasons.

In this study the emphasis is on real populations, on observed mortality, and on observed survival rates at different life stages. The number, size, and distribution of the samples made it practical and valid to develop a composite representation of mortality and survival in the Laysan Albatross.

RESULTS

Eggs and Chicks

Survival of eggs to hatching and of chicks to fledging is shown in Table 1. Complete information could be gathered only in the 1964-1965 season, and, as discussed elsewhere, this season was atypical. Hatching success averaged 64 percent (55 to 73). Survival to 6 to 8 weeks averaged 62 percent (54 to 68), and survival to fledging was 64 percent (49 to 78).

Mortality of chicks in the first few weeks after hatching equalled only zero to 2 percent of the eggs laid, or 1 to 3 percent of the chicks hatched. Mortality for the full nest period (egg to fledging) varied from 22 to 51 percent (mean 36). Loss of chicks equalled 3 to 17 percent of the eggs laid and varied from 4 to 24 percent of the chicks hatched. The data for 1964 indicate a 9-percent loss of chicks exposed to risk in the nest.

Fledglings during Departure from the Colony

The sample of 4,492 fledglings recorded on the beaches in July made up 26 percent of the 17,362 fledglings banded in their colonies. Daily counts of young in the plot indicated that

TABLE 1
SURVIVAL OF LAYSAN ALBATROSSES FROM EGG TO FLEDGING

EGGS		PERCENTAGE* OF CHICKS THAT SURVIVED TO:		
YEAR LAID	NUMBER	HATCHING	6 TO 8 WEEKS	FLEDGING
1961	619	—	—	78
1962	626	70	—	53
1963	708	73	—	70
1964	350	55	54	49
1966	628	61	61	—
1968	475	70	68	—
Weighted Average		64	62	64

* Percentage of number of eggs laid.

27 percent had left before the beach search began on 3 July. Thus, the sample of 4,492 represented 36 percent of the chicks (12,682) that could have been expected to leave during our recapturing on the beach.

Four hundred and eight, or 3.2 percent, of these departing chicks were found dead. The detailed data are available in H. I. Fisher and M. L. Fisher (1969: 187, table 7). Because some carcasses of young, banded birds were encountered in the bushes behind the beaches, we estimated that approximately 3.5 percent of the fledglings failed to gain the water.

The mortality of the young immediately after leaving the shore is problematical. Sharks of several species are believed to be the greatest danger, but the extent of their kill is speculative. We did see many, apparently healthy, active fledglings taken by sharks. In July 1962, from a low-flying helicopter, I counted 37 large sharks in the lagoon. That same month our baited hooks caught a 12-foot shark, a 9-foot, and a 7-foot one. We recovered 13 fledgling albatrosses from the stomach of the first shark, 6 from the second, and 7 from the third shark.

Not knowingly included in any of the above data are the fledglings that died of exhaustion, exposure, or starvation *on the water* in the lagoon or beyond the reef in their first days away from land. Their bodies may have floated to sea or been consumed by sharks.

On the above basis we estimated that total mortality during departure was nearly 10 percent.

Juveniles

Comparisons between the mean survival of the same age classes in samples of juveniles of different years are not always possible because of the chronology of our periods of recaptures (Table 2). Note, however, the close agreement (42 and 45 percent) of the 10-year-olds of 1961 and 1962 and of the 11-year-olds (41 and 44 percent) of 1960 and 1961. Some differences in survival of offspring of different years may be indicated in certain of the apparently anomalous statistics. A greater percentage of 8-year-olds of 1960 survived than of 7-year-olds of 1961, for example. The lesser observed survival of 3-year-olds of 1961 than of 4-year-olds of 1960 is a reflection only of the fact that not all 3-year-olds return to the colony.

There is some variability between the two islands in observed survival. In the 1960 sample, Sand Island consistently exhibited rates 10 to 15 percent lower than Eastern, but the 1961 and 1962 samples on the two islands did not differ significantly in survival. The "discrepancy" in the 1960 class is a direct effect, we believe, of the continuation of the albatross control program (H. I. Fisher 1966a) on Sand Island between 1960 and January of 1964. There was never any similar "control" on Eastern Island, and the program on Sand was limited to a narrow edge along the runway after the winter of 1963-1964.

The data for the plot also indicate a lower survival, caused by the nearby antennas.

With these explanations of variants in the

TABLE 2
SURVIVAL OF LAYSAN ALBATROSSES FROM FLEDGING TO 12 YEARS OF AGE

SAMPLE	NUMBER	PERCENTAGE SURVIVING TO:			
		1964-1965	1968-1969	1971-1972	1972-1973
1960					
Sand Island					
Antenna Field 1	684	56	51	39	33
Eastern Island Plot	277	—	58	46	41
Quarters	250	71	64	48	44
South Pier	318	77	64	51	43
Total	1,529	64*	57*	44*	38*
1961					
Sand Island					
Antenna Field 1	1,001	—	58	47	42
Antenna Field 2	500	60	57	46	40
Eastern Island Plot	469	—	48	39	37
Quarters	100	55	51	38	38
South Pier	301	65	55	47	42
Total	2,371	61*	55*	45*	41*
1962					
Sand Island					
Antenna Field 1	500	—	60	52	46
Officers' Country	1,500	—	—	—	39
Eastern Island					
Quarters	350	—	61	48	47
South Pier	750	—	57	47	40
Total	3,100	—	59*	49*	42*

* Average percentages weighted for varying sample sizes.

TABLE 3
AVERAGE MAXIMUM ANNUAL MORTALITY IN
LAYSAN ALBATROSSES FROM FLEDGING TO 12 YEARS
OF AGE, BY PERCENTAGE OF SAMPLE

NUMBER AND YEARS	SAMPLE YEAR		
	1960	1961	1962
Number	1,529	2,371	3,100
Years			
First 4	9.0	—	—
First 6	—	—	6.8
4 to 8	1.8	—	—
8 to 10	—	4.0	—
9 to 11	4.0	—	—
First 10	—	—	5.8
First 11	—	5.4	—
First 12	5.2	—	—

data, we see that the information shows good agreement between the samples of the same age

classes from various locations on the two islands. We may note in Table 2, if we interpolate from all years and all samples, that a mean of 64 percent of the banded fledglings survived to 4 years of age, 59 percent to 6 years, 55 percent to 7, 57 percent to 8 years, 49 percent to 9 years, 42-45 percent to 10 years, 41-44 percent to 11 years, and 38 percent to 12 years.

Viewed in another way (Table 3), mortality in the first 4 years averaged 9 percent per year of the original sample and 6.8 percent in each of the first 6 years. It was 1.8 percent per year in years 4 to 8, and 4.0 percent annually in years 8 to 11. During the first 12 years after leaving the nest, Laysan Albatrosses died at the rate of 5.2 percent per year. Mean annual mortality in years 13 to 15, inclusive, was 2.6 percent among 960 albatrosses.

TABLE 4

ANNUAL MORTALITY OF LAYSAN ALBATROSSES OF UNKNOWN AGE AND BREEDING IN THE STUDY PLOT

NUMBER AND YEARS	MORTALITY*	
	MALES	FEMALES
Number	917	988
Years		
1961-1962	1.9	2.8
1962-1963	7.0	4.9
1963-1964	8.1	8.2
1964-1965	4.9	7.9
1965-1966	7.7	5.2
1966-1967	8.5	6.1
1967-1968	6.7	7.5
1968-1969	3.1	6.4
1969-1970	2.4	2.8
1970-1971	2.8	3.2
1971-1972	4.9	4.9
Means	5.3	5.4

* Percentage of original sample.

TABLE 5

AVERAGE ANNUAL MORTALITY OF LAYSAN ALBATROSSES OF UNKNOWN AGE AND BREEDING IN THE SOUTH OF PIER AREA

SAMPLE	NUMBER	PERCENTAGE OF ORIGINAL SAMPLE		
		1963-1968	1963-1971	1963-1972
2	700	6.0	5.8	6.3
3	700	—	4.6	5.3

Breeding Birds of Unknown Age

The mean annual mortality observed in the plot was 5.3 percent (1.9 to 8.5) among males and 5.4 percent (2.8 to 8.2) among females (Table 4). The two samples of breeding birds from South of Pier had mean annual mortalities of 6.3 and 5.3 percent (Table 5).

In some seasons there appeared to be nearly 100 percent difference in the mortality rates of the sexes—1962-1963, 1964-1965, and 1968-1969, for example (Table 4). There was an irregular variation over the years in both sexes. However, annual rates for males between the 1962-1963 and 1967-1968 seasons, except in 1964-1965, were consistently above the mean rates. The rates for females were at or above the overall mean from the 1963-1964 to the 1968-

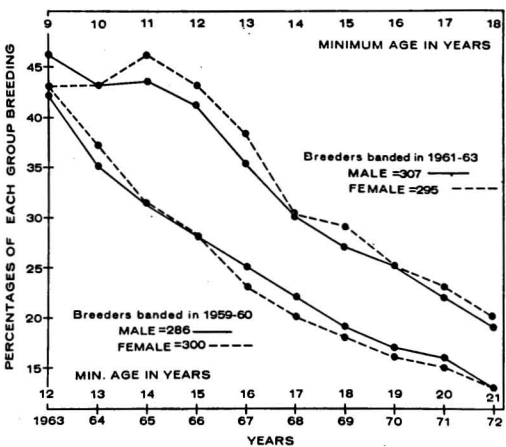


FIGURE 1. Survival of two samples of breeding Laysan Albatrosses assumed to be at least 8 years old at time of banding.

1969 season. Before and after these periods, the rates in both were significantly lower.

The “poor” years for breeding by experienced albatrosses—the seasons of 1964-1965 and 1968-1969 when breeding populations were lowest—have been alluded to previously. Mortality in males during these seasons was less than average, and that for females was significantly above the 11-year mean.

Survival of these breeders of a minimum age of 8 years at banding is shown in Figure 1. The upper curves represent plot breeders and the lower ones, breeders in the South of Pier sample. Except for years 9 to 11, the curves agree closely in indicating that (1) there is no consistent sexual variation in survival, (2) survival rates increase after the 14th year, (3) 41 to 43 percent survive to a minimum of 12 years of age, (4) 30 percent survive to 14 years, (5) 25 percent survive to 16 years, and (6) 18 to 20 percent survive to 18 years. The lower curve indicates a 13-percent survival to 21 years. There is also some indication of a decreased survival rate after 20 years, but this may be only an annual variant rather than a trend.

DISCUSSION

Egg Loss

In 1971 I found that egg loss by Laysan Albatrosses during the egg-laying periods of eight different seasons varied from 3.4 to

16.0 percent. The weighted mean of 7.2 percent compares well with the 6 percent per month reported by Rice and Keynon (1962: 372). The egg-laying period coincides with the first half of the incubation period, and if such rates of loss had continued for the entire incubation time, total egg loss would have approximated 12 to 15 percent, which, however, is less than half that shown in Table 1.

The anomaly is explained in part by the fact that Table 1 does not include the 1965–1966 and 1969–1970 seasons of my earlier study (1971a) because we could not be there to check hatching success. These were seasons of high breeding numbers and low egg loss during the laying period. Secondly, as I pointed out (1971a: 37), desertions, which are a primary cause of egg loss, may occur in great numbers in a short time; as many as 24 percent of all desertions may occur in a single storm. Most winter storms hit the breeding grounds between mid-December and March, and losses caused by them might be expected to be greater in the last half of incubation. Desertions by first-time breeders occur mostly in the middle of the incubating period.

Although my data for 1964–1965 indicate a fairly constant loss during incubation, the storms came early in 1964–1965. If the catastrophic seasons are omitted, losses in the first month of incubation are near 3 to 6 percent and are approximately 25 percent in the last half of incubation. Thus, the total of 28 to 31 percent is in fair agreement with the 36 percent in Table 1, if one considers that the great annual variations make averages relatively meaningless.

These variations make very difficult any valid comparisons with other, shorter term studies that also showed widely divergent results. For example, Westerskov (1963: 808) stated that losses among 101 eggs of the Royal Albatross on Campbell Island could not have been greater than 13 percent and that there was a 14-percent loss of 48 eggs laid on Taiaroa Head. Tickell (1968: 43) found a 28-percent loss of eggs among Wandering Albatrosses, which compares well with the suggested loss in Laysans. Harris (1973: 494) stated that hatching success in the Waved Albatross varied from 10 to 56 percent in 1970 and 1971 among different colonies on the Galápagos Islands, but

catastrophic losses appear to be almost typical of this species.

Ricklef's paper of 1969 would lead one to expect egg losses in the Procellariiformes to approximate 2 percent per day (1.3 to 2.8), but these intimations apparently are based on only one species, the Madeiran Storm Petrel, *Oceanodroma castro*, studied by Allan (1962), and the egg loss is not separately stated for that species (p. 28). Further, Harris (1969b: 131–132) reported much lower mean losses for this petrel—40 percent (32 to 59). The long incubation period of most Procellariiformes is incompatible with daily losses of the magnitude suggested by Ricklef. The Laysan, for example, would hatch only 16 percent of the eggs laid, if even Ricklef's minimal loss figures were used.

J. Fisher (1952: 342) found that egg loss in the Fulmar (30 to 60 percent) varied indirectly with the size of the colony.

I showed (1971a) that losses of eggs laid by older and experienced Laysans ranged from 23 to 32 percent, whereas eggs of younger, inexperienced birds suffered losses ranging from 34 to 54 percent. Harris (1969b) observed a similar phenomenon among *O. castro* breeding on the Galápagos.

Although one might expect egg loss to be greatest shortly after laying, as Dunnet, Anderson, and Cormack (1963: 8) found in *Fulmarus glacialis*, this is true only for the inexperienced Laysan Albatrosses. There is little need to repeat here my 1971 discussion of the timing and causes of egg loss in the Laysan. The data covered years of high and low breeding populations and thus include whatever "norms" are likely for degree and cause of loss.

It is apparent, even from the incomplete evidence available, that egg loss among the birds in the order Procellariiformes may be highly variable interspecifically and that it may vary intraspecifically with geographical location, season, colony, and biological maturity of the pair.

Chicks in the Nest

Sheehan (1951) reported a 90-percent loss of Laysan chicks 1 year on Sand Island and gave a "rough estimate" of 35 to 40 percent on Eastern Island. He noted that the high rate on

Sand Island occurred mostly because of aircraft movements and other human activity. Hadden (1941) estimated that 10 percent of the young had died between the ages of 1 and 6 months.

Downes et al. (1959: 62) reported that only 40 of 70 Black-browed Albatrosses, *Diomedea melanophris*, chicks hatched on Heard Island reached "... their final moult." Sorenson (1950) found that chick mortality among the Royals was heaviest in the first week after hatching—nearly 50 percent of the total—and that only a few died after the guard phase. Pinder (1966) also reported heaviest losses occurring shortly after hatching in *Daption capensis*. Such mortality is apparently not uncommon among sea birds. It may reach 44 percent in some species (*Uria lomvia*, Tuck 1960: 158, for example).

Our observations of the Laysan Albatross tend to corroborate the posthatching phase as being the time of greatest chick mortality, although the data are not identifiable in Table 1, and the differences in rates are very small. Mortality is essentially flat from hatching to fledging in the Laysan.

However, in the last week of July and the first week of August, mortality among chicks remaining in the colony is very high, 90 percent in some years. Hadden (1941: 34) wrote that about 5 percent of the chicks died at this time, but it is not clear whether he meant 5 percent of those hatched or of those then in the colony. These deaths, though large in number and conspicuous, are not as important as the percentages might indicate; fewer than 5 percent of the total number of fledglings remain in the colony in these weeks (H. I. Fisher and M. L. Fisher 1969: 186, 215) and these young birds are mostly from eggs laid late in the season by first-time breeders. Some other fledglings are simply undernourished at this time. It is not known whether the poor condition of these latter results from the earlier death of one or both parents or whether some surviving pairs, perhaps stimulated by the lateness of the season or the absence of other pairs feeding chicks, desert their chicks. The latter thought gains some support from the deaths of three chicks known to be the offspring of experienced pairs that survived to breed the following year. However, most of the deaths of chicks under

daily surveillance in 1964–1965 and 1968–1969 occurred because of the known death of one or both parents. A generally insufficient food source for oceanic birds, as theorized by Ashmole (1963), may be reflected in fewer Laysans attempting to breed, but not in greater losses of chicks. The 1964–1965 season (Table 1) may illustrate this point, although it is possible that more food became available late in the season. Breeding numbers and hatching success were the lowest recorded, but chick losses were only 6 percent, compared with 3 and 17 percent in the two previous seasons.

The observation by Galtsoff (1933) of hundreds of dead, nestling Laysans in July on Pearl and Hermes Reef may well relate to an unusual "crash" in midsummer food supplies. It is curious that I observed a similar massive mortality on the same islet in the same month 30 years later. No causative factor could be found, but the dead chicks were very emaciated.

Elliott (1957: 573) noted that large numbers of nestling *Diomedea chlororhynchus* died on Tristan Island after 3 weeks of exceptionally dry weather, but it is difficult to see a relationship between these events, and no such observations have been made on Midway.

High winds may cover chicks with sand or force waves onto the low breeding islands, and heavy rainstorms may flood nests; though the losses may be high in the limited areas affected, they constitute but a small percentage of total chick losses. Peterson (1967) suggested that hordes of mosquitoes may have forced large numbers of incubating Waved Albatrosses to desert their chicks in one season, and Harris (1969a) noted that several breeding failures in this species occurred in years of heavier-than-average rainfall. Whether the rainfall acted directly on the chicks or whether it was simply a concomitant of adverse conditions at sea is not known.

Parent Laysans trample a few chicks, and an occasional neighboring chick is killed by an adult preparing to feed its own chick. Norway rats, *Rattus norvegicus*, on Midway are responsible for the deaths of some young chicks already in a weakened state. It is unlikely that the Polynesian rat, *Rattus exulans*, absent from Midway but reported by Kepler (1967) to kill

incubating Laysans on Kure Island, has any widespread effect.

Albatross chicks pick up and swallow many foreign objects. Pieces of ceramic insulators, bits of copper wire, broken glass, electric line fuses, small toothpaste tubes, various plastic bottle caps, and flashlight batteries and flashbulbs have been recovered from dead birds or from ejected oral pellets which also contained squid bones and undigested parts of small coelenterate animals. Some of these may be picked up by adults at sea and fed to the chick along with natural food objects, although these materials are not usually found in undisturbed colonies away from tidal action and storm waves. The number of deaths they caused is unknown.

The skeletal remains of a nestling frequently surround a number of these objects. John R. Hendrickson (personal communication, 10 Dec 1969) also noted this phenomenon and suggested that successive generations of chicks might be affected by the same objects. This certainly is a possibility because (1) nests are always in the same place; (2) the bones of a chick that died the previous season are often incorporated into the nest, as would be the objects; and (3) Laysan chicks constantly pick up and swallow almost anything within reach.

Social dominance (Fretwell 1969) is a much less likely factor in the mortality of young Laysans. Late in the nestling period the chicks do wander from the home nest, establish "subnests," form companion groups, and squabble with chicks in neighboring groups. In this time the older, larger, more adventurous chicks do dominate the late-hatched youngsters. Because the surviving chicks return to land by age-cohorts in future years, and to the same site, any dominance hierarchy established among nestlings might become operative then and have an effect on mortality. There are several problems attendant to this hypothesis for Laysans. One unknown, of course, is whether the hierarchy persists for the 4 to 6 years the birds are away from the colony and from each other and becomes effective when the birds first return to establish territories and to find mates. Some contact between members of these subcolony groupings (H. I. Fisher and M. L. Fisher 1969: 189) does occur

in the early visits to the colony by juveniles; it must be very limited because of the briefness and infrequency of the visits and because not all juveniles return before their 4th year. We did observe subcolony associations in egg-laying dates and in the activities of feeding chicks (H. I. Fisher and M. L. Fisher 1969: 189), but there is no way of knowing whether these activities of breeding birds resulted from the associations they had formed at least 7 years earlier during their fledgling periods.

A second problem with "status" as a factor in the mortality of Laysans is they are not really social birds. They apparently are solitary in feeding at sea, although they may rest or feed briefly in very loose aggregations. There is little evidence of sociality on land, other than that between members of young dancing groups or the members of the pair.

Finally, there is thus far no reason to think that the site of the territory within the colony has any influence on survival or reproductive success. Until supporting data are found, we cannot presume social hierarchies that force subdominant individuals into theoretically less suitable sites or that cause earlier deaths for their offspring or for themselves.

Although disease has been suspected in some deaths, no certain evidence, to my knowledge, has been found of viral or other infections in albatrosses. Macdonald and Conroy (1972) have suggested that *Diomedea melanophrys* chicks may periodically suffer great losses from some form of puffinosis and may be an intermediate host between shearwaters and penguins in the South Orkney Islands.

F. T. Lynd, a veterinary pathologist of the Hawaiian Department of Agriculture and Forestry, wrote to Dr. Ernest H. Willers, State Veterinarian, on 28 October 1959, stating that in four nestling Laysans "blood studies were not remarkable except for a blood parasite; *Lecocytozoon* [sic] sp." However, the late Dr. Richard R. Kudo of Southern Illinois University examined more than 100 blood smears from Laysans of various ages and found no parasites of any kind. Worm parasites have been found in the digestive tract (H. I. Fisher, unpublished), but in no birds were they considered to be the cause of death. The numerous members of the Mallophaga known to inhabit

the feathers of these albatrosses (Ward and Downey 1973) have never been associated with mortality, and Rowan (1951: 152) believed that ticks and mites associated with the Yellow-nosed Albatross, *Diomedea chlororhynchus*, were of no significance to the bird.

The negative nature of these observations is perhaps more of a reflection of our lack of knowledge of the diseases of albatrosses than an indication of the freedom of these animals from disease, especially since it is known that Fulmars (Macdonald et al. 1967) and Manx Shearwaters (Miles and Stoker 1948) are at least intermittently affected by puffinosis.

Nest Failure (Egg and Chick)

It is difficult to evaluate the fragmentary information on nest loss in the Laysan, especially since there is so much annual variation. Rice (1959: 15) reported a 50-percent loss among 164 eggs on Sand Island and 24 percent among 2,676 eggs laid on Eastern Island. Military activity may well have been a primary factor on Sand Island. However, both percentages are within the range found in this study. Rice (1959) also reported losses of from 42 to 67 percent between the egg and fledgling stages in the Laysan. Kepler (1967: 429) noted a 52-percent loss on Kure Atoll in the 1964–1965 season, which is essentially what we found that same season on Midway.

Tickell (1968: 43) stated that 59 percent of the eggs of the Wandering Albatross produced flying chicks. Westerskov (1963: 808) thought that approximately 75 percent of the Royal Albatross eggs yielded fledglings, and Richdale (1952: 149) calculated from Sorenson's data on Campbell Island a nest success of 64 percent for this species. However, Richdale also reported only a 31-percent success among 64 eggs laid at Taiarora Head. Harris (1973: 494) observed that nest success in the Waved Albatross varied from 5 to 82 percent among different colonies during a 3-year period and calculated (p. 506) an average 25.4-percent success "... in the years when young are raised."

These levels of nest success in other albatrosses are within the ranges suggested for the Laysan, and they tend to be higher than those for other procellariiform species. Allan (1962)

found 43 percent for *Oceanodroma castro*, which lies within the 13 to 66 percent (mean 50) observed by Harris (1969b). Harris reported only 20-percent nest success for *O. tethys*, but the data are questionable, as he indicated. The Cape Pigeon fledges about 33 percent (Pinder 1966), and the Snow Pigeon, *Pagodroma nivea*, perhaps 40 to 45 percent (Prévost 1964: 101).

Losses of eggs by Laysan Albatrosses are more significant in total nest failures than are losses of chicks. Whereas 30 percent of the eggs laid in "non-catastrophic years" (Table 1) fail to hatch, only an additional 6 to 8 percent of the eggs laid fail to produce a flying young because of deaths after hatching. Expressed in other terms of mortality—30 percent (27 to 39) of the eggs exposed to risk "die," and only 12 percent (4 to 24) of the chicks hatched die in these years.

Mortality of Fledglings during Departure

The observed loss of 3.5 percent of the fledglings departing in July may not be representative of the entire departure period. Those leaving prior to 3 July may have been more successful; most of them were offspring of older, experienced breeders and hence perhaps better fed and stronger. Further, the gathering of sharks in the lagoon apparently increases in late June and July, so that the later departing chicks may have been subjected to heavier predation.

Schauinsland (1899: 63) noted that Laysan fledglings had a difficult time surviving in the lagoon of Laysan Island and that many died on the beaches, especially when there was a heavy, inshore surf. Rice (1959: 16) estimated that "two-thirds" of the fledglings that reached the flying stage left the island successfully. And Tuck (1960: 153) thought that perhaps 10 percent of his *Uria lomvia* were lost when they first went to sea.

We regard our estimate of an approximate 10 percent loss as a reasonable guess for the departure stage. Since this period when young of all species depart from parental care and begin to fend for themselves is so critical, it is disheartening to find so little information about it. In the case of the Laysan Albatross, at least, the still unknown factors causing mortality at

that time may combine to exert a tremendous selective pressure.

Mortality of Juveniles

Nelson (1964) believed that 80 percent of the juvenile North Atlantic Gannets, *Sula bassana*, die before breeding age, an average 6-percent annual mortality. Carrick and Ingham (1967: 167) reported that 10 percent of the fledged chicks of Royal Penguins at Macquarie Island survived to 6 years, which is perhaps an average age of first breeding in that species.

The data on Procellariiformes are few. Richdale (1952) reported that 6 of 11 chicks of the Royal Albatross were in the colonies in later years. Robertson and Wright (1973: 49) found that 60 percent of 85 chicks of *Diomedea epomophora* returned to the colony "at least 4 years later." Tickell (1968) wrote that 38 percent of 656 chicks of the Wandering Albatross were in the colony 4 to 6 years later. He also stated (p. 44) that "... about 50 percent of the Wanderer fledglings leaving Bird Island survive to return to the breeding grounds." Harris (1973) reported mean losses ranging from 5.7 to 7.9 percent per year during the juvenile period in Waved Albatrosses. However, Harris did not make it clear whether or not the total years included in the means encompassed all the prebreeding years, although he did indicate (p. 506) that the observed mortality "... must include some young which died before fledging." He also stated that "... once the young fledge they survive as well as adults." I am unable to confirm this from the data given.

Since the rates of survival of juvenile Laysan Albatrosses are based upon the original numbers of fledglings banded and since perhaps 10 percent of these are lost at the time of first departure, it is evident that the survival rate is higher than that indicated by the raw data for these early years at sea. We may conclude, if the estimated, minimal losses at departure are excluded, that at least 71 percent of the young that reach the open sea survive to 4 years of age, 65 percent to 6 years, and 63 percent to the initiation of breeding at 8 years.

The significant difference in mean annual mortality between the first 4 years and the second 4 years of the juvenile's life correlates

well with differences in the events of the life cycle.

In its first 4 years, the Laysan Albatross is on the open ocean, except for a few, short visits to the breeding colonies during the springs of its 3rd and 4th years (H. I. Fisher and M. L. Fisher 1969). Of its life on the ocean, we know only where it spends a great deal of its time (H. I. Fisher and J. R. Fisher 1972). We cannot assume that there is differential annual mortality in these 4 years, although Tuck (1960) working on Murres, Coulson and White (1959) on Kittiwakes, and Tickell (1968) on Wandering Albatrosses did so assume. Coulson and White suggested that 21 percent of the Kittiwakes may die in the 1st year after leaving the nest.

During its second 4 years, the Laysan, by now presumably somewhat experienced in food gathering and survival at sea, turns increasing attention to the breeding colony. Repeated and longer visits are made to the home colony. The males establish territories and the females visit from male to male. Courtship takes up much time.

The rigors occasioned by youth, inexperience, and strange surroundings and predators at sea cause relatively heavy losses. By the time the young bird begins to come regularly to the colony, it has overcome much of the adverse impact of life at sea, but on land it is also subject to new stresses—territorial acquisition and pair formation. These, however, do not seem to be either direct or significant factors in mortality, although both activities require a great deal of energy. The albatrosses probably do not come to the colony unless they are well nourished, and the spacing of the activities (H. I. Fisher and M. L. Fisher 1969) permits ready replenishment of energy at sea (H. I. Fisher 1967). Because of its adaptations to life at sea, the young Laysan might have lesser mortality than in the first 4 years, whether or not it came to land. However, the terrestrial part of the juvenile period presents fewer disadvantages and no predators, which may well be responsible for the lower death rate.

Mortality of Breeders

The agreement in observed mortality rates in large samples from two different colonies sup-

ports the conclusion that mean annual mortality is between 4 and 6 percent among breeders. These composite rates for breeders of all ages are near those previously suggested—5 percent (Rice 1959: 18) and "...not greater than 8.6 percent" (Rice and Kenyon 1962: 383). For various reasons, the data on other albatrosses are not very satisfactory. Lack (1954: 92) calculated from Richdale's data of 1952 that adult mortality was 3 percent annually in the Royal Albatross, but I question its validity because it was based upon a small, growing population, one that has continued to increase partly by immigration from other colonies (Robertson 1973).

Tickell (1968: 44) reported a 5.4-percent annual rate in 64 males and a 3.1-percent rate in an equal number of female Wandering Albatrosses. On the basis of a 2-year observation of 138 adult *D. melanophris*, Tickell and Pinder (1967: 315) suggested a 6.7-percent rate. Harris (1973: 505) found mortality in adult Waved Albatrosses that ranged from a rate of 4.1 to 6.4 percent per year, but he believed that perhaps 5.0 percent was the maximum among breeders. The validity of the data in these studies is open to some question because not all breeders of these species nest in successive years or even return to the colony.

Richdale and Warham (1973: 25) observed a mean annual mortality of 11 percent among 159 *D. bulleri* between 1948 and 1972, without seeing any evidence of sexual differences in survival. As the authors noted, the rate is probably too high because the recapture of these birds was not a primary part of their investigation and there was no consistent effort to catch them.

Other species of Procellariiformes exhibit rates similar to those reported for albatrosses. For example, Harris (1966) gave 6 percent as the annual rate for *Puffinus puffinus*. Richdale (1963: 84) reported a mean annual rate of 8.5 percent among breeding and associating pairs of Sooty Shearwaters, *P. griseus*, and Dunnet, Anderson, and Cormack (1963) calculated an approximate 6-percent mean annual mortality rate among adult Fulmars.

Other large marine birds are reported to have comparable rates among breeders, but Lack (1966: 248) believed that the 6-percent annual

mortality observed by Nelson (1964) in adult *Sula bassana* was the lowest for any species of bird except for his observation of 3 percent in *Diomedea epomophora*.

The only indication in the literature of differential mortality between the sexes in the Procellariiformes is that of Tickell, noted earlier. My data (Table 4) indicate no significant, long-term sexual variation among breeding Laysans, and the slight difference I noted between the sexes in young breeders may be the result of the females' averaging a year older at the time of first breeding.

The apparent, great sexual variation in mortality during some years does emphasize the danger of relying on data from short-term studies, but there is another interpretation for this variation. During the years of generally high mortality (1962 to 1968, inclusive) females twice had rates nearly 100 percent greater than did males, and both occasions were during "bad" years for albatrosses. It is tempting to speculate that the increased rates in females were related to their relatively greater and more rapid energy demands during egg-formation in years when the food supply immediately preceding the breeding periods may have been inadequate.

It is important in analyzing the data in Table 4 to keep in mind that females are 1 year older than males at the onset of reproduction and that this may cause them to lag 1 year in exhibiting comparable mortality. Thus, if the mortality for males of any given year is compared with that for females in the following year, the comparison is between birds of different ages but with a similar number of years of breeding experience. For example, in the seasons of 1964–1965 through 1966–1967, the 5.2-percent rate for females in 1965–1966 is much closer to the males' 4.9 percent in 1964–1965 than it is to the males' 7.7 percent in 1965–1966. The same relationship holds for subsequent seasons. This may indicate that mortality in the breeding years is more dependent upon the number of times the stresses of reproduction have been undergone than it is upon age alone. Unfortunately, it is impossible to obtain a sample of birds that have lived long periods without reproducing.

It is significant that mortality was not higher

during the poor years of 1964–1965 and 1968–1969. The explanation may be, as H. I. Fisher and M. L. Fisher (1969) found, that large numbers of experienced breeders forego attempts to breed in these years. Although they may be found in the colony, especially late in the incubation period, they are below normal in weight (H. I. Fisher 1967: 374–375). It seems possible that lower-than-usual food resources available during the pre-egg stage of the season produce a positive effect on survival of experienced breeding birds. By not attempting to reproduce when food is scarce, even for the individual bird, these breeders which are so valuable for the maintenance of the species are spared the perhaps fatal stresses occasioned by breeding and rearing a chick. There is, of course, an adverse effect on the species; it loses 1 year's complement of offspring from these birds. However, this loss is probably more than offset by the survival of the adults and the retention of their already demonstrated reproductive potential for future years.

Slightly more than 40 percent of all breeding Laysans of estimated ages lived to a minimum of 12 years (Figure 1). Thirty-eight percent of 1,529 birds of known age survived to 12 years, a close agreement that adds some credence to our method of estimating ages.

The apparent absence of mortality, or at least the presence of very low mortality, in the 9th to 11th years in the top curves on Figure 1 requires explanation. The birds represented can be assumed to be young ones just initiating nesting, and I have shown (1975b) that mortality in the first 3 years of reproduction is very low.

Survival rates begin to increase near the 14th year of life (the 6th or 7th of breeding), which also agrees with the conclusions I reached in the study of young breeders of known age. The validity of this observed increase is further strengthened by the fact that it was found at two different times (1965 and 1968) in two different colonies.

If the survivorship lines in Figure 2 are projected beyond the last year of observation and a constant rate of survival is assumed, it can be observed that Laysan Albatrosses may have a breeding life expectancy of at least 15 years. The bottom curves of Figure 1 may

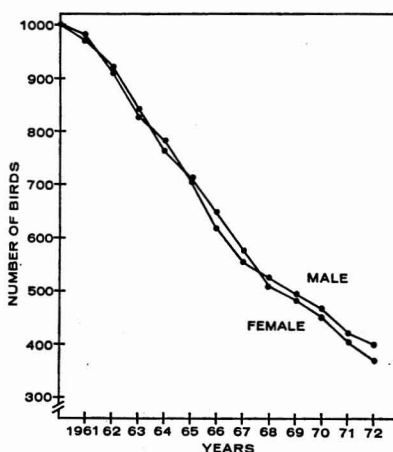


FIGURE 2. Survival of a composite sample of breeding Laysan Albatrosses assumed to represent all breeding ages in the colony.

provide evidence of decreased survival after the 20th year, the 12th of reproduction. If this be true, the expectancy may be less. However, the observed, overall, mean annual mortality of 5.3 to 6.0 percent among breeding Laysans indicates a reproductive life of at least 17 years.

There is some information on the breeding life expectancy in other procellariiform birds. Hudson (1966) suggested that *Daption capensis* may have 16 to 20 years and *Pagodroma* some 14 to 24 years, but, as the author noted, these figures may be subject to considerable errors because of the small samples, the band losses, and the great annual variation in the extent and intensity of recapture efforts. Orians' findings (1958) may be used to show adult expectancies ranging from 13 to 33 years for *Procellaria puffinus*. Richdale's data of 1963 on *Puffinus griseus* indicate a 12- to 16-year adult life. And Dunnet, Anderson, and Cormack (1963) estimated that their 236 *Fulmarus glacialis* had a reproductive life ranging from an observed 4.3 years to a calculated 14 to 18 years.

Lack (1954: 106) concluded that the probability of survival was essentially independent of age, once adulthood was reached. This concept has not been tested in sea birds, at least to my knowledge, and those who have commented upon it (Hudson 1966: 63, for example) have been more concerned with increased mortality resulting from "senility" than with

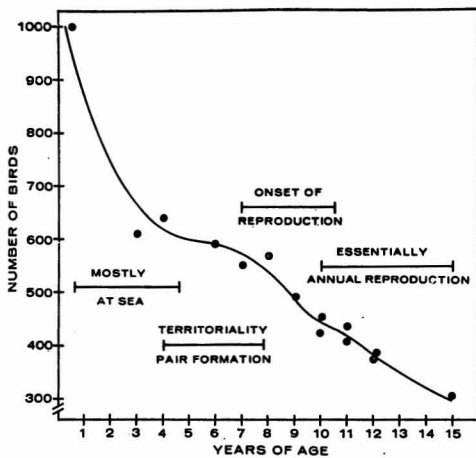


FIGURE 3. The relationship between survival and the major events in the life cycle of Laysan Albatrosses.

the possibility of lesser mortality in aged but still reproductively active birds. Although the concept may be valid for relatively short-lived species, I suggest that its applicability to long-lived forms is much less certain. The breeding albatrosses of this study exhibited a marked decrease in mortality in their 13th to 15th years. As a population they had been breeding for 5 years prior to the change and continued to breed for the remaining 4 to 7 years that they continued to be under observation. The only variable appeared to be their ages. Further, the possible decrease in survival after 20 years appears to be age-related.

Certain aspects of Lack's logical suggestion that individuals that initiate breeding at an age less than the average for the species are subject to greater mortality would seem to be in conflict with the view that mortality is independent of age in adults. But perhaps Lack did not view these early breeders as being fully "adult." The question is moot as far as Laysans are concerned. Only those that began breeding 2 years earlier or 2 years later than usual showed somewhat decreased survival (H. I. Fisher 1975b). Further, Lack's postulated increased mortality in young breeders did not appear in Laysans until the 3rd to 6th years of reproduction and appeared to be independent of the age at which they first began to breed and independent of sex. The mean annual mortality during the first nine breeding seasons of young birds

was actually lower (4.0 percent for males and 3.7 percent for females) than for the breeding population as a whole (5.3 to 6.3 percent).

One can only speculate about the causes of mortality at sea. Sharks and perhaps large fishes take an unknown toll. Some Laysans are lost to fishing nets and lures, but their numbers must be insignificant. It might be expected that oil on the surface would immobilize albatrosses, as Bourne, Parrack, and Potts (1967), for example, have reported. It may, but the only oiled Laysans we observed on Midway were known to have gotten the oil from runways, roads, and water catchment basins. Further, any oil, natural or otherwise, is rather rapidly destroyed or dissipated by evaporation, emulsification, autooxidation, or oxidation by microorganisms (Pilpel 1968) under the highly aerobic conditions found in the pelagic zones utilized by Laysan Albatrosses.

Southern Hemisphere albatrosses are frequently destroyed in some numbers by winter storms (Whitlock 1927; Kinsky 1968; and Imber 1971, for example), but most of the deaths take place as the albatrosses are driven ashore. The North Pacific habitat of the Laysan has few shores, and the birds do not frequent them, except for those of the small breeding islands. However, Whitlock attributed some of the onshore deaths to weakness brought on by the birds' inability to feed during bad weather. Kinsky believed that the stage of the molt influenced the extent of the storm-caused mortality. These are possible factors in the case of the Laysan, but there is no supporting evidence. And the incidental observations we have made of molt indicate that the Laysans that return to breed have completed their molt of flight feathers by November, which is prior to the winter storms. The molt of the body feathers occurs in March to May, after the worst weather, at least in those breeders and juveniles in the colony then.

Wurster and Wingate (1968) attributed the declining population of the Bermuda Petrel, *Pterodroma cabow*, to the presence of foreign, chemical residues in its food supply. Pollutant residues apparently are not yet large enough in the Laysan Albatross or the Black-footed Albatross, *Diomedea nigripes*, to reduce breeding success or to cause death (H. I. Fisher 1973).

We can be confident in saying that most Laysans die at sea. Returned juveniles and breeding birds seldom die of natural causes in the colonies.

Figure 3 is based upon mean mortality rates but here combined and weighted for age and sample size. It illustrates the survival of a hypothetical sample of 1,000 Laysan Albatrosses from the time of their departure from the island at approximately 6 months of age to the time of their prime reproductive activity at age 15 years.

Approximately 30 percent of the fledglings in the nest survive to the age of 15 and have 6 to 8 breeding years. It is evident that this high rate of survival of fledglings into the prime reproductive years is associated with the one-egg clutch of the species and the absence of replacement clutches. Equally apparent and significant is the inherent resiliency of the species—its ability to recover when populations suffer major catastrophes. The long life of the individual, the absence from the colony of some breeders in any one year, or indeed at any one time of the year, and the fact that the immature offspring representing at least 7 years of reproduction of the species spend most of their time far at sea all contribute to this ability.

Two further factors may be mentioned. All Laysans return close to their home islands and colonies, and the number of such islands and their geographical distribution are very limited. These factors cause the breeding islands to serve as a collecting mechanism for survivors, preventing widespread scattering of survivors and aiding in the maintenance of colony numbers above any possible failure level.

SUMMARY

Eggs and Chicks in the Nest

Hatching success was 64 percent (55 to 73). Egg loss in the 1st month of incubation averaged 3 to 6 percent, and it rose an additional 25 percent in the 2nd month in some years. Loss of eggs was highly variable annually and was primarily dependent upon the number of desertions by incubating adults, which in turn was dependent upon the occur-

rence of winter storms at critical times and upon the age and experience composition of the breeders of that year. Many first-time breeders failed to complete incubation.

Fledging success varied from 49 to 78 percent (mean 64) of the eggs laid in different years. Chick losses ranged from 3 to 17 percent of the eggs laid, with an essentially flat rate from hatching to fledging.

The primary cause of chick deaths was believed to be the death of one or both parents. High winds, floods, rats, and ingestion of foreign materials may collectively cause significant losses. There was no evidence to link disease or social status with mortality of Laysan chicks. Catastrophic losses of unknown origin occurred occasionally.

Expressed in the usual mortality rates, 30 percent (27 to 39) of the eggs exposed to risk "died," and perhaps 12 percent (4 to 24) of the chicks hatched were lost in a "normal" year.

Approximately 35 percent of the eggs laid produced chicks that survived to breeding age.

Fledglings during Departure

About 3.5 percent of the young birds were known to die as they left the colonies and moved onto the beaches. Most of the losses were occasioned by starvation; the fledglings were not fed during this time, and the stresses of departure quickly depleted their energy reserves.

An equal percentage of the fledglings may have been lost to sharks, the only known predators at this time. Some additional fledglings soon died on the water, bringing the total mortality during the first departure from land to nearly 10 percent.

The factors resulting in mortality in this phase of the life cycle may exert a significant selective pressure against late-departing fledglings that were the offspring of the younger, less experienced, and "less-proven" breeders.

Juveniles

Approximately 71 percent of the juveniles that survived their first departure from the island lived to 4 years of age, 65 percent to 6

years, and some 63 percent to age 8 when most of the birds first began to breed.

Mean mortality rates of these successful fledglings were quite different for the first and last halves of their 8-year juvenile period—6.8 versus 1.8 percent per annum, respectively. The higher rate was correlated with inexperience, new surroundings at sea, and sharks. The lower rate in the later years resulted from increased experience in food-getting and survival at sea and the increased time on land where the biological stresses appeared to be less.

Breeders

The mean annual mortality, expressed as percent of the original sample of albatrosses banded, averaged 5 to 6 percent during the 9 and 11 years during which a total of 3,305 breeding albatrosses of unknown age were under observation.

Mean annual mortality was 5.3 percent for males and 5.4 percent for females. There was no consistent, sexual difference, but females lagged 1 year in exhibiting rates comparable to those of males, probably because the females were 1 year older when they entered the breeding population.

Mortality of breeding females was much greater than that of males in 2 years of low breeding numbers, which may have been correlated with the females' greater energy requirements during the early phases of annual reproduction. However, the rates for both sexes were no higher than usual, and it was thought that the failure of many experienced breeders to attempt reproduction eliminated the additional reproductive stresses in years of low availability of food, which served to increase survival rates and preserve these experienced breeders and their reproductive capabilities for future years.

Survival rates increased after the 14th year of life, the 6th or 7th of breeding. Not until after 20 years of age was there any indication of a decreased rate of survival. This evidence from birds that had bred for several years before and after their 14th year suggested that survival of adult Laysan Albatrosses is not entirely independent of age, at least during the years of prime reproductive activity. However, repro-

ductive requirements were judged to be more significant than age in causing mortality prior to the 14th year.

Approximately 40 percent of these breeding albatrosses survived to a minimum of 12 years, 30 percent to 14 years, 25 percent to 16 years, 20 percent to 18 years, and perhaps 13 percent lived to 20 years of age.

Laysan Albatrosses may have a breeding life expectancy of some 16 to 18 years.

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